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Evaluation of morphological attributes as response variables to perennial competition for 4-year-old black spruce and jack pine seedlings

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The sensitivity of seedling morphological attributes to changing competition levels was evaluated on 4-year-old black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) seedlings to determine the most appropriate response variables to be used in the assessment of early plantation performance. A total of 720 seedlings (360 per species) were sampled between 1987 and 1989, covering a range of stock types, soil textures, and competition levels. A competition index, derived from hemispherical photographs, provided an estimate of incident radiation received by each sampled seedling. Seedling stem volume at time of planting was used as a covariate in the regression analyses. Stratification by plantation was done to account for variations in site quality. The results from this study demonstrated that total height or current height increment were not reliable for quantifying individual seedling response to interspecific competition for 4-year-old black spruce or jack pine plantations. Overall, the most consistent response variable was total seedling dry weight. Coefficients of determination ranged from 0.116 to 0.534 for black spruce and from 0.601 to 0.810 for jack pine across the range of sites and stock types. If it is inappropriate to determine total seedling dry weight, root collar diameter would be the best substitute. Correlation coefficients between these two variables were 0.897 for black spruce and 0.912 for jack pine.

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La capacité des caractères morphologiques des semis à réagir à différents niveaux de compétition a été évaluée sur des semis de l'épinette noire (*Picea mariana* (Mill.) B.S.P.) et du pin gris (*Pinus banksiana* Lamb.) âgés de 4 ans dans le but de déterminer quelles variables sont les plus appropriées pour juger de la performance des jeunes plantations. Au total, 720 semis, 360 de chaque espèce, représentant plusieurs types de stock, de textures de sol et de niveaux de compétition, ont été échantillonnés entre 1987 et 1989. Un indice de compétition dérivé à partir de photographies hémisphériques a fourni un estimé de la radiation incidente reçue par chaque semis échantillonné. Le volume de la tige du semis au moment de la plantation a servi de covariable dans les analyses de régression. Les plantations ont été stratifiées pour tenir compte des variations dans la qualité de la station. Les résultats de cette étude démontrent que la hauteur totale ou l'accroissement courant en hauteur ne sont pas fiables pour quantifier la réponse de semis individuels à la compétition interspécifique pour des plantations d'épinette noire ou de pin gris âgées de 4 ans. Dans l'ensemble, la meilleure variable était le poids sec total des semis. Les coefficients de détermination variaient de 0,116 à 0,534 pour l'épinette noire et de 0,601 à 0,810 pour le pin gris selon les types de stocks et les stations. S'il n'est pas possible de déterminer le poids sec total des semis, le diamètre au collet est le meilleur choix. Les coefficients de corrélation entre ces deux variables étaient de 0,897 pour l'épinette noire et de 0,912 pour le pin gris.

[Traduit par la revue]

Introduction

The growth response of outplanted nursery stock to perennial competition is of critical economic importance in many forest regions of North America (Walstad and Kuch 1987). The major investments being made in tree improvement, stock production, site preparation, and planting may produce few dividends if follow-up tending is neglected, particularly on highly productive sites. Eradicating competition is expensive, necessitating a selective application of herbicides based on a thorough understanding of the relationship between plantation productivity and competition level. This understanding requires both a measure of the competition level occurring on a site as well as a measure of relevant tree responses.

Morphological attributes based on a series of individual tree growth measurements may act as response variables when evaluated against given levels of competition. Since the early 1970s, a wide variety of competition indices have been developed in attempts to quantify the degree of interference caused by the surrounding vegetation (Bella 1971; Daniels 1976; Zedaker 1982; Brand 1986*a*). Commonly, studies of this type have relied on easily measured morphological attributes (i.e., height or relative height growth) as subject tree response variables. Recent evidence has shown that stabilization of height growth increment generally occurs 5 to 8 years after planting or once total height is greater than 1.5 m (Brand and Weetman 1986; Thrower 1986; Omule and Krumlik 1987) for a variety coniferous species. Oppenheimer *et al.* (1989) demonstrated that height responses of slash pine to changing competition regimes was not significant until the fourth growing season. Height increment may be too insensitive to changing levels of competition to identify growth suppression during the initial phase of plantation development, thus providing little assistance to forest managers in making early tending decisions.

Research has been conducted on a limited number of

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TABLE 1. Site and competition characteristics present on sampled plantations

Plantation No.	FEC site type	Sand[c] (%)	Clay[c] (%)	Competitor[a] density (stems/ha)	Competition index[b]			
					Min.	Max.	Mean	SE
1	S8C	40.4	29.6	28 085	18.4	86.0	54.7	2.05
2	SS7	44.0	25.5	30 116	19.3	82.9	50.4	2.04
3	S3C	65.1	16.2	24 966	21.2	91.9	53.7	2.37
4	S5C	29.0	55.2	41 096	18.6	86.4	52.8	2.15
5	S1C	75.4	8.5	31 154	31.0	87.2	59.3	2.01
6	S3C	65.8	11.1	38 445	23.8	86.3	64.6	1.86
7	S9C	31.1	36.0	57 193	43.8	93.0	77.9	1.51
8	S1C	49.5	20.9	42 306	11.8	92.4	47.6	3.02
9	S3C	59.2	16.9	50 101	15.6	88.8	46.4	2.49
10	S4C	52.6	21.1	28 042	19.8	93.4	59.6	3.11
11	S1C	58.6	19.9	28 583	14.1	90.7	58.5	3.14
12	S4C	53.6	20.9	27 527	19.6	81.6	47.6	2.17

[a]Based on perennial competitor counts from 60 subplots per plantation each with an area of 6.158 m^2.
[b]Calculated from 60 photographs per plantation using eq. 1.
[c]Based on 60 samples per plantation taken from the upper B-horizon.

species to identify the most responsive morphological variables to changing levels of competition. Zutter *et al.* (1986) determined that stem diameter and biomass were more responsive to reductions in interfering vegetation than was height for 1- and 2-year-old loblolly pine (*Pinus taeda* L.) seedlings. They also identified a correlation between total needle surface area and groundline basal area. Specific leaf area of foliage (Brand 1986*b*) and production of interwhorl buds (Tappeiner *et al.* 1987) have been found to represent promising developmental characteristics for assessing competition stress in young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings. Kellomäki (1981) identified that different light intensities changed the allocation of growth among tissues of 20-year-old Scots pine (*Pinus sylvestris* L.) trees.

In Ontario, 80% of the current artificial regeneration budget is expended on black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) (Anonymous 1987). Reforested areas are considered to be effectively regenerated when they have passed the stage of establishment and have been declared free-to-grow. A stand is free-to-grow when it meets the following criteria (Ontario Ministry of Natural Resources 1988): (*i*) a minimum stocking standard; (*ii*) a minimum height requirement; and (*iii*) when it is essentially free of competition that impedes growth. It seems apparent that this measure of seedling growth must relate to the current competition level if an accurate assessment of the free-to-grow status is to be made. It has been demonstrated that this relationship can differ between species (Waring *et al.* 1977; Harrington *et al.* 1984), as well as between different age-classes (Tucker and Emmingham 1977; Shelton and Switzer 1984). Therefore, the objective of this study was to evaluate the sensitivity of various seedling response variables to a range of competition levels for both black spruce and jack pine during early (4 years after outplanting) plantation establishment and growth. The most sensitive response variable could then be used to evaluate early plantation performance in relation to occurrence of competition.

Methods

The data used for this study were collected from six 4-year-old black spruce plantations in 1987 and from six 4-year-old jack pine plantations in 1988. These plantations were established on boreal mixedwood sites, as defined by Whitney and McClain (1981), consisting of 60–70% conifer (upland black spruce, jack pine, and some white spruce (*Picea glauca* (Moench) Voss) and 30–40% hardwoods (trembling aspen (*Populus tremuloides* Michx.) and white birch *Betula papyrifera* Marsh.)) by basal area. The previous stands were clear-cut and ranged from 1.0 to 20.0 ha of continuous cutover, using traditional cut and skid operations. These areas were site prepared using barrels and chains during the fall prior to planting. No weed control had been carried out prior to measurement. All 12 plantations were located in the North Central Region of Ontario between 48°32′N and 49°53′N latitude and between 85°15′W and 92°15′W longitude. Species and stock types for these plantations were as follows: (*i*) plantation 1-3, black spruce overwintered (paperpot) containerized stock; (*ii*) plantation 4-6, black spruce bare-root (1.5 + 1.5) stock; (*iii*) plantation 7-9, jack pine overwintered (paperpot) containerized stock; and (*iv*) plantation 10-12, jack pine bare-root (2 + 0) stock.

The plantations represented a wide range of soil textures and site types for each of the species and stock types studied, within the context of the Forest Ecosystem Classification (FEC) developed for the North Central Region of Ontario, Canada (Table 1). The FEC site types ranged from S9C clay to S1C coarse sand (Ontario Institute of Pedology 1985). A wide assortment of perennial shrubs and tree species develop from root suckers on these site types. The tree stratum is dominated by trembling aspen and white birch, with the shrub stratum consisting primarily of beaked hazel (*Corylus cornuta* Marsh.), speckled alder (*Alnus rugosa* (Du Roi) Spreng.), mountain maple (*Acer spicatum* Lam.), and willow (*Salix* spp.).

A total of 720 seedlings, 60 from each of the 12 plantations studied, were randomly selected using a Cartesian coordinate system. A 300-g soil sample was taken from the upper B horizon near the base of each seedling sampled. In the laboratory, the soil samples were air dried, sieved (2 mm), and analyzed for clay fraction (Bouyoucos hydrometer method) and total nitrogen (macro-Kjeldahl procedure).

Vertical hemispherical photographs, using a single-lens reflex camera and a 7.5-mm fish-eye lens, were taken at the base of the seedlings' current leaders. These photographs were taken in mid-July, when most of the height growth and foliage development was complete for the seedlings and perennial competitors. From these photographs, both the percent open sky (blocks 0% of sunlight) and the percent opaque canopy (blocks 100% of sunlight) were calculated using a PLANIX 7P planimeter. The remaining area between the two extreme light regimes was classified as transparent canopy. This area represented a combination of small open sky

TABLE 2. Summary of coefficients of variation (%) of the means for growth response variables from 4-year-old black spruce and jack pine seedlings

Response variable	Black spruce plot No.						Jack pine plot No.					
	1	2	3	4	5	6	7	8	9	10	11	12
Total height	18.7	24.4	24.1	19.1	20.5	16.6	22.0	17.2	19.1	21.8	16.6	15.0
Current height increment	41.8	43.5	37.2	35.8	34.7	31.8	54.7	20.1	23.5	30.0	24.4	21.1
Crown volume	71.4	99.2	59.1	72.4	72.3	44.9	162.7	76.5	90.4	95.7	76.4	58.8
Root collar diameter	25.9	33.3	25.5	24.6	32.0	18.6	35.3	31.1	33.5	36.2	30.3	23.2
No. of buds	59.3	73.1	61.5	63.4	53.2	45.2	73.9	66.3	71.4	98.0	74.1	69.6
Needle spacing	25.3	28.8	28.6	26.5	25.6	27.9	30.9	22.1	22.8	26.6	22.7	21.9
Specific needle area	17.0	10.9	17.4	14.9	13.7	14.9	19.7	19.1	14.9	17.2	23.4	19.6
Total seedling weight	54.2	71.7	58.5	55.6	54.9	36.8	81.8	61.5	76.4	93.7	70.6	57.1
Total foliage weight	53.6	71.4	58.5	59.1	54.1	37.3	75.2	61.9	76.5	99.3	73.7	58.3
Current foliage weight	58.5	75.5	64.5	63.4	56.3	40.3	89.3	67.1	80.2	105.3	80.4	60.1
Branch weight	71.6	91.5	65.7	66.8	68.8	43.4	100.4	71.6	94.8	115.2	90.6	83.7
Stem weight	52.8	65.8	59.4	48.4	59.0	38.7	76.1	59.5	67.5	79.5	60.0	45.2
Root weight	70.6	73.9	65.3	61.4	54.4	42.3	117.2	67.8	87.3	103.7	78.3	62.1
Current radial increment	45.0	47.7	38.6	45.1	70.2	34.7	45.8	42.7	44.7	48.9	44.2	31.5
Total stem volume	60.9	94.1	63.8	60.3	76.9	44.1	104.2	66.1	77.5	86.8	73.3	56.0
Needle/soil N ratio	42.0	47.4	37.3	43.0	75.5	34.9	50.8	27.1	30.4	44.4	53.1	96.0

TABLE 3. Summary of coefficients of determination (r^2, adjusted for covariate) for growth response variables from 4-year-old black spruce seedlings regressed on a standard competition index

Response variable	Black spruce plot No.					
	1	2	3	4	5	6
Total height	$0.008_{(0.82)}$	$0.039_{(0.15)}$	0.291	$0.156_{(0.16)}$	$0.308_{(0.09)}$	0.057
Current height increment	$0.022_{(0.28)}$	$0.025_{(0.98)}$	0.163	$0.028_{(0.97)}$	$0.141_{(0.38)}$	$0.075_{(0.06)}$
Crown volume	$0.003_{(0.81)}$	0.116	0.140	0.402	$0.084_{(0.85)}$	$0.099_{(0.02)}$
Root collar diameter	0.133	0.243	0.494	0.418	0.528	0.289
No. of buds	$0.084_{(0.03)}$	0.183	0.392	0.384	0.172	0.203
Needle spacing	$0.010_{(0.51)}$	$0.029_{(0.22)}$	$0.032_{(0.57)}$	$0.003_{(0.73)}$	$0.007_{(0.55)}$	$0.012_{(0.48)}$
Specific needle area	$0.046_{(0.27)}$	$0.105_{(0.05)}$	0.162	0.175	0.168	$-0.035_{(0.37)}$
Total seedling weight	0.116	0.214	0.459	0.534	0.349	0.367
Total foliage weight	0.111	0.207	0.404	0.470	0.261	0.274
Current foliage weight	0.152	0.189	0.361	0.469	0.249	0.223
Branch weight	$0.081_{(0.03)}$	0.178	0.397	0.461	0.219	0.360
Stem weight	$0.085_{(0.06)}$	0.177	0.492	0.430	0.488	0.353
Root weight	0.123	0.240	0.402	0.560	0.332	0.298
Current radial increment	0.200	0.110	0.563	0.071	0.316	0.205
Total stem volume	$0.081_{(0.06)}$	0.153	0.425	0.470	0.519	0.269
Needle/soil N ratio	$0.016_{(0.67)}$	$0.085_{(0.04)}$	$0.039_{(0.14)}$	$0.036_{(0.18)}$	$0.004_{(0.67)}$	$0.041_{(0.75)}$

NOTE: Coefficients of determination are subscripted by significance levels exceeding 0.01. Individual seedling stem volumes at time of planting were used as a covariate in all regression models presented.

TABLE 4. Summary of coefficients of determination (r^2, adjusted for covariate) for growth response variables from 4-year-old jack pine seedlings regressed on a standard competition index

Response variable	Jack pine plot No.					
	7	8	9	10	11	12
Total height	0.456	0.215	0.536	0.415	0.357	0.231
Current height increment	$0.066_{(0.27)}$	0.131	$0.268_{(0.04)}$	0.230	0.127	0.222
Crown volume	0.342	0.270	$0.546_{(0.04)}$	0.431	0.352	0.355
Root collar diameter	0.563	0.724	0.821	0.795	0.721	0.667
No. of buds	0.553	0.577	0.804	0.800	0.555	0.381
Needle spacing	$0.035_{(0.73)}$	$0.039_{(0.87)}$	0.241	$0.022_{(0.37)}$	$0.026_{(0.25)}$	$0.083_{(0.70)}$
Specific needle area	$0.024_{(0.51)}$	$0.045_{(0.27)}$	$0.099_{(0.06)}$	$0.086_{(0.08)}$	$0.052_{(0.25)}$	$0.054_{(0.21)}$
Total seedling weight	0.648	0.707	0.810	0.720	0.645	0.601
Total foliage weight	0.669	0.713	0.817	0.748	0.573	0.618
Current foliage weight	0.630	0.686	0.816	0.783	0.596	0.655
Branch weight	0.650	0.673	0.771	0.670	0.579	0.542
Stem weight	0.604	0.633	0.777	0.682	0.669	0.515
Root weight	0.560	0.632	0.746	0.590	0.601	0.552
Current radial increment	0.221	0.465	0.360	0.791	0.617	0.505
Total stem volume	0.594	0.606	0.788	0.684	0.643	0.867
Needle/soil N ratio	$0.010_{(0.53)}$	$0.051_{(0.10)}$	$0.001_{(0.85)}$	$0.032_{(0.19)}$	$0.010_{(0.47)}$	$0.039_{(0.15)}$

NOTE: Coefficients of determination are subscripted by significance levels exceeding 0.01. Individual seedling stem volumes at time of planting were used as a covariate in all regression models presented.

areas and larger opaque regions. During preliminary testing, it was determined that the transparent canopy blocked approximately two-thirds of the potential radiation intercepted by the canopy. Based on strong negative correlations with growth, the total canopy fraction was used to evaluate the seedlings' response variables. This competition index, derived from the hemispherical photographs, was as follows:

$$[1] \quad \text{competition index} = [\text{opaque \%} + (\text{transparent \%} \times 2/3)]$$

Table 1 summarizes the range of competition index levels present on the 12 sites studied.

After bud set in late August, each seedling was carefully excavated with the root system intact. Counts of needle scars were made from a 3-cm section taken from the central portion of the current leader. Needle spacing was then calculated as the number of needles per centimetre of leader growth. An additional 200 needles per seedling for black spruce and 100 needles per seedling for jack pine were selected from the central portion of the uppermost lateral branches and removed for nutrient analysis and for fresh leaf area determination. The projected area of these needle samples was measured with a Li-Cor 3100 area meter. The ovendry masses (dried for 48 h at 70°C) of the needle samples were later determined, and total nitrogen analyses were conducted. Specific leaf areas were calculated ($cm^2 \cdot g^{-1}$) and total height (cm), current height increment (cm), crown length (cm), crown width (cm), and root collar diameter (mm) were recorded. Cylindrical crown volumes (cm^3) were approximated by squaring the crown radius and multiplying by the crown length. The seedlings were then separated into current, 1-year previous, and remaining plant material for foliage, branch, and stem components. A basal disc was removed for ring analysis. Cylindrical stem volumes (cm^3) were approximated by squaring the root collar radius and multiplying by the total seedling height. All seedling biomass components were individually bagged and dried at 70°C for 48 h before dry weights (g) were determined. Table 2 provides a complete list of the 16 response variables tested, along with a summary of the degree of variation (coefficients of variation) exhibited by each variable for the species studied.

During preliminary regression analyses, possible non-normality or heteroscedastic patterns were identified for some response variables (i.e., biomass components) from scatterplots of residuals. A data normality test was performed using the Kruskal–Wallis test (Siegel 1956), and homogeneity of variances was examined by White's test (White 1980). No significant results occurred, therefore, untransformed variables were used in the subsequent regression analyses and evaluation of all response (dependent) variables. From scatterplots, based primarily on seedling root collar diameter versus the competition index [1], a total of 19 outliers were identified. From ring counts obtained from a basal disc, 17 of these outliers were found to be naturally regenerated seedlings 1 to 2 years older than the outplanted stock. Two seedlings were found to have severe damage unrelated to competition effects (i.e., insect damage, moose browse), which occurred after the initial selection process. All 19 outliers were removed from subsequent analyses.

Undetected interactions between factors such as, genetic, microsite (Cannell *et al.* 1984), size of planting stock (Mitchell *et al.* 1988), and planting quality (Burdett *et al.* 1984), as well as chance factors, can cause high variability in seedling performance. This variability makes it difficult to confidently determine the competition effects on an individual seedling basis. To account for some of this variation, analysis of covariance and stratification were applied. Individual seedling responses were adjusted for the influence of seedling size at the time of outplanting, defined by stem volume at time of planting. These adjusted values (depen-

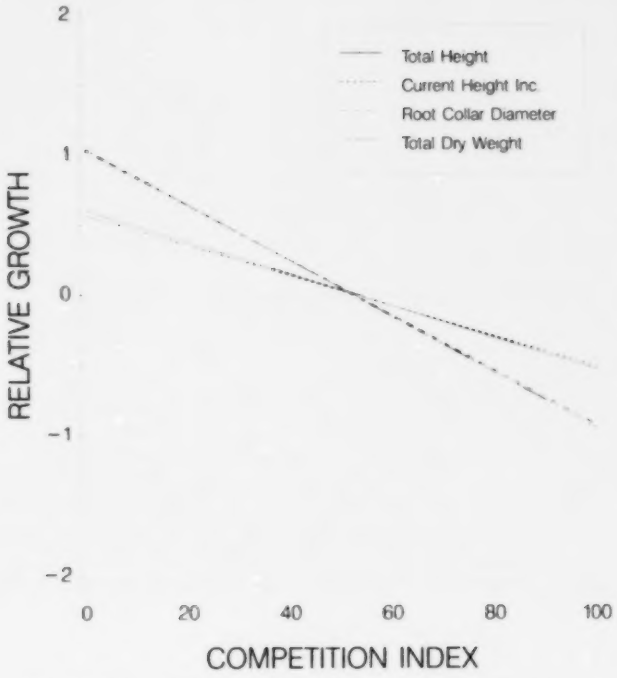

FIG. 1. Four regression lines depicting relative growth versus competition level for 4-year-old black spruce plantations (container stock). Inc., increment.

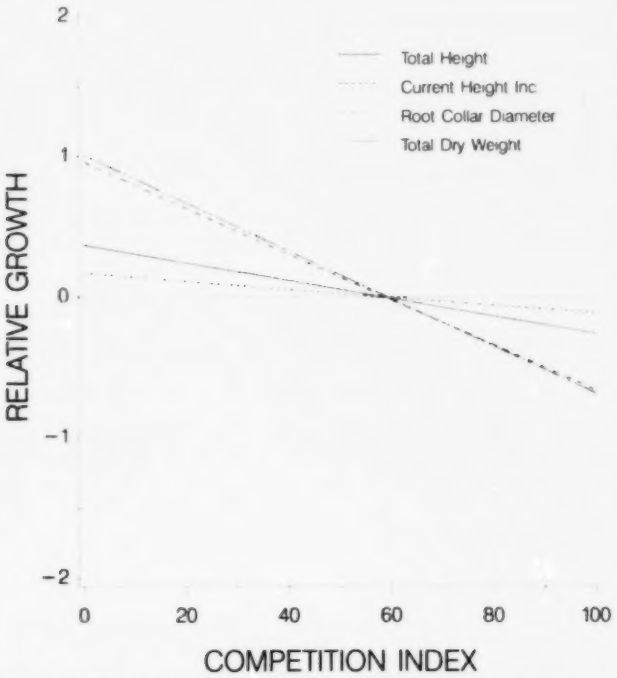

FIG. 2. Four regression lines depicting relative growth versus competition level for 4-year-old black spruce plantations (bare-root stock). Inc., increment.

dent variable) were then regressed against the competition index (independent variable). To account for variations in site quality, the data were stratified by plantation in the regression analysis.

Figures for each species and stock type were generated depicting the relationship of total height and current height increment (currently the most commonly used by forest managers when evaluating plantation performance), as well as root collar diameter and total seedling dry weight (the most consistent response variables tested) versus the competition index. To compare these four response variables on a common scale, standard deviates (Y-axis in figures) were calculated using the following formula (Snedecor and Cochran 1980):

[2] $$SD_i = (X_i - X_j)/s_j$$

where SD_i is the standard deviate for the ith individual, X_i is the value for the ith individual, X_j is the sample estimate of the mean for the jth response variable, and s_j is the standard deviation for the sample mean of the jth response variable. Sample size for estimates of means and standard deviations was approximately 60, but varied slightly for the 12 plantations because of the removal of 19 outliers.

These figures were used to illustrate the sensitivity of these four response variables to changing levels of competition. A regression line that exhibits little variation across the range of competition levels for any response variable would simply be $Y = 0$.

Results and discussion

An individual plant in a population of seedlings must become established and gain access to resources necessary for its future growth and development (Ross and Harper 1972). Since plants are immobile, they are forced to compete with their neighbours throughout their life. The term competition implies that the supply of environmental resources falls below the combined demands of the plants and that these resources are shared unequally based on the relative competitiveness of the plants (Harper 1964). Site resources include light, water, nutrients, and (or) physical growing space (Daniels *et al.* 1986). Therefore, as Goldberg and Fleetwood (1987) stated, the total competitive ability of any organism must consist of two distinct aspects: (*i*) competitive effect, which is the ability of an organism to reduce the performance of other organisms and (*ii*) competitive response or tolerance, which is the ability of an organism to continue to perform relatively well in the presence of competitors. It is this competitive tolerance that the present paper addresses. More specifically, it attempts to identify the morphological attributes most sensitive to competition 4 years after outplanting.

The lowest coefficients of determination were associated with those response variables that relate to moisture and nutrient status (Tables 3 and 4). These variables include needle spacing (Brand 1986*b*), needle/soil nitrogen ratio (Sutton 1969; Youngberg and Davey 1970), and specific leaf area (Zedaker 1983). It seems logical that a weak relationship with these variables exists if the seedlings are competing mainly for light, rather than for water and nutrients (Bleasdale 1966). Slightly better correlations, although still not significant, were associated with coarser sites where moisture retention is low. Although foliage morphology has been found to be strongly related to competition in Douglas-fir (Brand 1986*b*) and to a lesser extent in loblolly pine (Zutter *et al.* 1986), foliage morphology represents a poor performance variable for both black spruce and jack pine seedlings. It should be noted that the index used to evaluate seedling growth response quantified light regime rather than direct root competition. This approach is probably biased against those response variables related to root activity.

Coefficients of variation of the mean ranged from 15.0 to 24.1% for total seedling height and from 20.1 to 54.7% for current height increment (Table 2). These values are substantially lower than those reported for the response variables obtained through destructive sampling, which were as high as 117.2%. Figures 1 through 4 demonstrate that a weak linear relationship between relative shoot elongation (obtained from eq. 2) and competition level existed resulting in regression lines with minimal slopes and low coefficients of determination (0.008 to 0.536 for total height and 0.022 to 0.268 for current height increment), although some significant F-ratios ($p = 0.01$) were obtained (Tables 3 and 4). It has been demonstrated that coefficients of determination for regressions using height can be quite small at young ages for loblolly pine (Daniels *et al.* 1986; Zutter *et al.* 1986), but increase over time if competition stress is maintained (Daniels *et al.* 1986). Better relationships between height growth and competition index did exist for jack pine. Since jack pine is significantly more shade intolerant than black spruce (Ritchie 1987), reduced light conditions have started to affect the height growth for the former species (Figs. 3 and 4). Similar results with black spruce may occur if competition pressure is maintained over time.

Low coefficients of variation of the mean also existed for root collar diameter (18.6 to 33.3% for black spruce and 23.2 to 36.2% for jack pine), however, a strong linear relationship between this variation in radial growth and competition level existed. Coefficients of determination for root-collar diameter ranged from 0.133 to 0.528 for black spruce (Table 3) and from 0.667 to 0.821 for jack pine (Table 4). Slopes associated with the regression lines using relative root-collar diameter (obtained from eq. 2) averaged −0.018 for black spruce (Figs. 1 and 2) and −0.034 for jack pine (Figs. 3 and 4), indicating moderate sensitivity to changing levels of competition. These results are consistent with those found for loblolly pine. Zutter *et al.* (1986) documented increases in diameter of 43 to 323% for seedlings growing without herbaceous competition.

Significant results were obtained for total number of buds, with coefficients of determination as high as 0.804, but this was not consistent for the 12 plantations studied (Tables 3 and 4). In Douglas-fir plantations, Tappeiner *et al.* (1987) determined that bud production on the leader provided a reliable index of the effects of competition. However, interwhorl (foliar) buds represented a significant portion of these bud counts. These foliar buds have been found to be primary sinks for photosynthate (Waring and Schlesinger 1985). In Douglas-fir, interwhorl buds have been found to represent approximately 50% of the total crown foliage (Jensen and Long 1983). The fact that nodal buds are more common in both black spruce and jack pine probably explains our inconsistent results.

The response variables obtained through biomass determination produced consistent results across the range of sites and stock types (Tables 3 and 4). In competition studies dealing with the southern pines, total aboveground biomass and branch weight related closely to competition level (Zutter *et al.* 1986). Loblolly pine expresses dominance early and crowns develop rapidly, partitioning a large portion of biomass into branches (Fowells 1965). This is not the case for either black spruce or jack pine, which both exhibit slow early growth (Fowells 1965). For these species, the three most reliable response variables related to biomass production were total seedling dry weight, total foliage dry weight, and

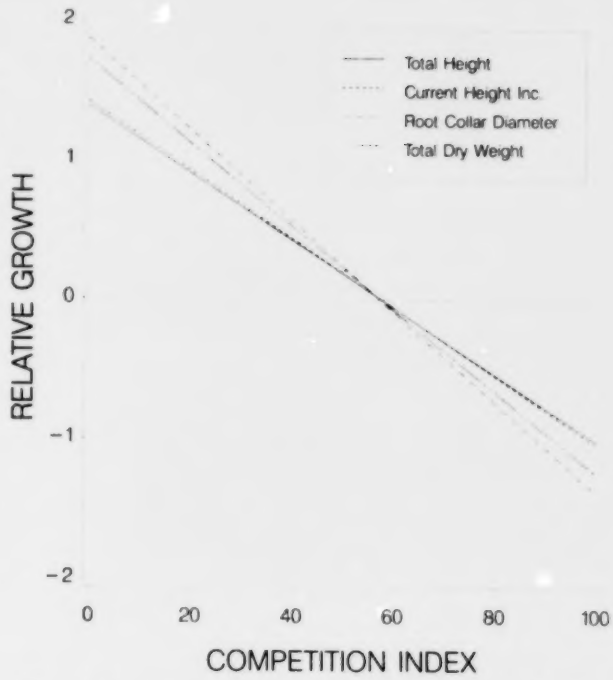

FIG. 3. Four regression lines depicting relative growth versus competition level for 4-year-old jack pine plantations (container stock). Inc., increment.

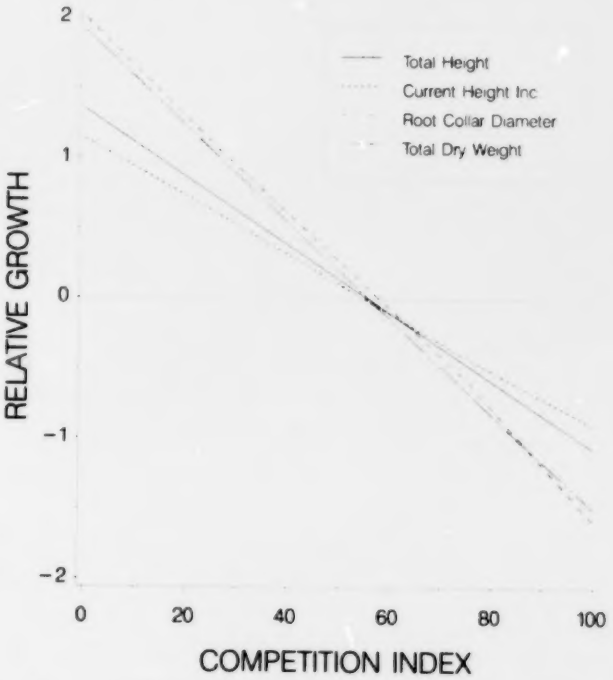

FIG. 4. Four regression lines depicting relative growth versus competition level for 4-year-old jack pine plantations (bare-root stock). Inc., increment.

TABLE 5. Correlation matrix illustrating the linear relationships (r) between various morphological attributes of 4-year-old black spruce and jack pine seedlings

	Total height	Current height increment	Root collar diameter	No. of buds	Total seedling weight
Total height	1.000 (1.000)	0.795 (0.856)	0.816 (0.837)	0.714 (0.658)	0.817 (0.767)
Current height increment		1.000 (1.000)	0.677 (0.734)	0.644 (0.588)	0.667 (0.657)
Root collar diameter			1.000 (1.000)	0.797 (0.855)	0.897 (0.912)
No. of buds				1.000 (1.000)	0.895 (0.899)
Total seedling weight					1.000 (1.000)

NOTE: Values are the correlation coefficients for the combined six plots for each species studied. $n = 351$ for black spruce; $n = 350$ for jack pine. Correlation coefficients for jack pine data are in parentheses.

current foliage dry weight. Coefficients of variation of the mean for these variables ranged from 36.8 to 75.5% for black spruce and from 57.1 to 105.3% for jack pine (Table 2). Up to 53.4% of this variation in black spruce (Table 3) and 81.7% in jack pine (Table 4) can be accounted for by the competition index. Slopes associated with the regression lines using relative total seedling dry weight (obtained from eq. 2) averaged -0.018 for black spruce (Figs. 1 and 2) and -0.032 for jack pine (Figs. 3 and 4). As with height growth, biomass production in jack pine appears to be more sensitive to changing levels of competition than in black spruce, which is more shade tolerant.

It appears that although a lack of sensitivity to increased competition pressure existed for shoot elongation, diameter growth and the production of biomass reflected significant variations in growth directly correlated with changes in competition level. From our earlier definition, total seedling biomass should be a good estimator of a plant's total competitive ability, since it normally reflects photosynthetic area (foliage weight), size of the root system (root weight), and structural dimensions (stem and branch weight); consequently, it serves to integrate the seedling's potential ability to exploit resources (Sievanen *et al.* 1988; Byrne and Wentworth 1988). Given the results of this study, it would seem reasonable to use total seedling dry weight as a response variable when defining seedling growth as outlined in criterion *iii* of the free-to-grow definition (see Introduction) when evaluating early plantation performance.

Destructive sampling and subsequent dry weight determination lend themselves more readily to research projects designed to study competition dynamics rather than to forest management practices. Foresters must be able to make rapid decisions concerning release treatments for their plantations. This time constraint negates the use of destructive sampling techniques that are costly and time-consuming. A simpler measurement that has a high correlation with total seedling dry weight would be beneficial. Relationships between prominent morphological attributes were examined in a correlation matrix and are summarized in Table 5. This matrix illustrates that from the easily measured morphological attributes, both root collar diameter and number of buds have the strongest relationships to total seedling dry weight. Correlation coefficients of 0.897 (black spruce) and 0.912 (jack pine) for root collar diameter and 0.895 (black spruce) and 0.899 (jack pine) for number of buds were reported.

Collecting bud counts may not incur great capital investments in equipment, but it can be a time-consuming procedure in the field as individual seedlings can have over 2000 buds. Therefore, root collar diameter may be the best substitute parameter for total seedling dry weight if destructive sampling is inappropriate. It should be noted that a weaker relationship between the competition index and seedling growth was exhibited by the shade-tolerant black spruce, and therefore, may need further refinement for use with this species.

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ANONYMOUS, 1987. Tree improvement master plan for Ontario. Queen's Printer for Ontario, Toronto.

BELLA, I.E. 1971. A new competition model for individual trees. For. Sci. **17**: 364–372.

BLEASDALE, J.K.A. 1966. Plant growth and crop yield. Ann. Appl. Biol. **57**: 173–182.

BRAND, D.G. 1986*a*. A competition index for predicting the vigour of planted Douglas-fir in southwestern British Columbia. Can. J. For. Res. **16**: 23–29.

———— 1986*b*. Competition-induced changes in developmental features of planted Douglas-fir in southwestern British Columbia. Can. J. For. Res. **16**: 191–196.

BRAND, D.G., and WEETMAN, G.F. 1986. Standards for regeneration establishment in Canada: a case study for Douglas-fir. For. Chron. **62**: 84–90.

BURDETT, A.N., HERRING, L.J., and THOMPSON, C.F. 1984. Early growth of planted spruce. Can. J. For. Res. **14**: 644–651.

BYRNE, S.V., and WENTWORTH, T.R. 1988. Relationship between volume and biomass of early successional vegetation and the prediction of loblolly pine seedling growth. For. Sci. **34**: 939–947.

CANNELL, M.G.R., ROTHERY, P., and FORD, E.D. 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. Ann. Bot. (London), **53**: 349–362.

DANIELS, R.F. 1976. Simple competition indices and their correlation with annual loblolly pine tree growth. For. Sci. **22**: 454–456.

DANIELS, R.F., BURKHART, H.E., and CLASON, T.R. 1986.

A comparison of competition measures for predicting growth of loblolly pine trees. Can. J. For. Res. **16**: 1230–1237.

FOWELLS, H.A. 1965. Silvics of forest trees of the United States. Dep. Agric. Agric. Handb. No. 271.

GOLDBERG, D.E., and FLEETWOOD, L. 1987. Competitive effect and response in four annual plants. J. Ecol. **75**: 1131–1143.

HARPER, J.L. 1964. The nature and consequence of interference amongst plants. Genet. Today Proc. Int. Congr. 11th 1963. pp. 465–482.

HARRINGTON, T.B., TAPPEINER, J.C., II, and WALSTAD, J.D. 1984. Predicting leaf area and biomass of 1- to 6-year-old tanoak (*Lithocarpus densiflorus*) and pacific madrone (*Abrutus menziesii*) sprout clumps in southwestern Oregon. Can. J. For. Res. **14**: 209–214.

JENSEN, E.C., and LONG, J.N. 1983. Crown structure of a codominant Douglas-fir. Can. J. For. Res. **13**: 264–269.

KELLOMAKI, S. 1981. Effects of the within-stand light conditions on the share of stem, branch, and needle growth in a twenty-year-old Scots pine stand. Silva Fenn. **15**: 130–139.

MITCHELL, R.J., ZUTTER, B.R., and SOUTH, D.B. 1988. Interaction between weed control and loblolly pine, *Pinus taeda*, seedling quality. Weed Technol. **2**: 191–195.

OMULE, S.A.Y., and KRUMLIK, G.J. 1987. Juvenile height growth of four species on four sites in the $CWH6_1$ variant. Canada – British Columbia Economic and Regional Development Agreement Forest Resource Development Agreement No. 007. Government of Canada, Province of British Columbia, Victoria.

ONTARIO INSTITUTE OF PEDOLOGY. 1985. Field manual for describing soils. 3rd ed. Ontario Institute of Pedology, Guelph.

ONTARIO MINISTRY OF RESOURCES. 1988. Policy on regeneration effectiveness and free-to-grow declaration. Ontario Ministry of Natural Resources, Toronto. Policy No. FR140101.

OPPENHEIMER, M.J., SHIVER, B.D., and RHENEY, J.W. 1989. Ten-year growth response of midrotation slash pine plantations to control of competing vegetation. Can. J. For. Res. **19**: 329–334.

RITCHIE, J.C. 1987. Postglacial vegetation of Canada. Cambridge University Press, New York.

ROSS, M.A., and HARPER, J.L. 1972. Occupation of biological space during seedling establishment. J. Ecol. **60**: 77–88.

SHELTON, M.G., and SWITZER, G.L. 1984. Variation in the surface area relationships of loblolly pine fascicles. For. Sci. **30**: 355–363.

SIEGEL, S. 1956. Non-parametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York.

SIEVANEN, R., BURK, T.E., and EK, A.R. 1988. Construction of a stand growth model utilizing photosynthesis and respiration relationships in individual trees. Can. J. For. Res. **18**: 1027–1035.

SNEDECOR, G.W., and COCHRAN, W.G. 1980. Statistical methods, 7th ed. Iowa State University Press, Ames.

SUTTON, R.F. 1969. Form and development of conifer root systems. Commonw. For. Bur. Tech. Commun. No. 7.

TAPPEINER, J.C., II, HUGHES, T.F., and TESCH, S.D. 1987. Bud production of Douglas-fir (*Pseudotsuga menziesii*) seedlings: response to shrub and hardwood competition. Can. J. For. Res. **17**: 1300–1304.

THROWER, J.S. 1986. Estimating site quality from early height growth of white spruce and red pine plantations in the Thunder Bay area. M.Sc.F. thesis, Lakehead University, Thunder Bay.

TUCKER, G.F., and EMMINGHAM, W.H. 1977. Morphological changes in leaves of residual western hemlock after clear and shelterwood cutting. For. Sci. **23**: 195–203.

WALSTAD, J.D., and KUCH, P.J. 1987. Forest vegetation management for conifer production. John Wiley & Sons, New York.

WARING, R.H., and SCHLESINGER, W.H. 1985. Forest ecosystems—concepts and management. Academic Press, New York.

WARING, R.H., GHOLZ, H.L., GRIER, C.C., and PLUMMER, M.L. 1977. Evaluating stem conducting tissue as an estimator of leaf area in four woody angiosperms. Can. J. Bot. **55**: 1474–1477.

WHITE, H. 1980. A heteroscedasticity-consistent covariance matrix estimator and a direct test for heteroscedasticity. Econometrics, **48**: 817–838.

WHITNEY, R.D., and MCCLAIN, K.M. (*Editors*). 1981. Boreal mixedwood symposium. Canadian Forestry Service, Great Lakes Forest Research Centre, Sault Ste. Marie, Ont. COJFRC Symp. Proc. O-P-9.

YOUNGBERG, C.T., and DAVEY, C.B. 1970. Tree growth and forest soils. Oregon State University Press, Corvallis.

ZEDAKER, S.M. 1982. Growth and development of young Douglas-fir in relation to intra- and inter-specific competition. Ph.D. thesis, Oregon State University, Corvallis.

———— 1983. The competition release enigma: adding apples and oranges and coming up with lemons. *In* Proceedings of the 2nd Biennial Southern Silvicultural Research Conference. *Edited by* E.P. Jones. USDA For. Serv. Gen. Tech. Rep. SE-24. pp. 357–364.

ZUTTER, B.R., GJERSTAD, D.H., and GLOVER, G.R. 1986. Effects of interfering vegetation on biomass, fascicle morphology, and leaf area of loblolly pine seedlings. For. Sci. **32**: 1016–1031.